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PRELIMINARY NOTES ON SOME AMERICAN CHALICOTHERES[1]

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COMPARATIVELY little is known of the American forms of the Chalicotherioidea,— an extinct family of mammals. Professors Marsh,[2] Cope,[3] Scott,[4] and Osborn[5] have from time to time published brief accounts of the few fragments available, but nothing comprehensive on the osteological structure of these unique animals has been accessible in America until quite recently.

A short time ago Dr. W. J. Holland, Director of the Carnegie Museum, gave the writer permission to submit to the Seventh International Zoological Congress some brief notes on the splendidly preserved remains of *Moropus clatus* Marsh which were secured by the Carnegie Museum from the Agate Spring Fossil Quarry in Sioux County, Nebraska.

This important fossil quarry has yielded much material which is now being prepared for study and publication. The quarry is located in the valley of the Niobrara River in the Lower Harrison horizon, and was evidently the bed of a stream, or perhaps the shore of a small lake, during a portion of the Miocene time. The bones were imbedded in a comparatively thin stratum of soft sandstone which was quarried out in large blocks. These were properly

[1] Read before the Seventh International Zoological Congress, Boston, Mass., August 21st, 1907.

[2] Am. Jour. Science, Vol. XIV, pp. 249–251, 1877.

[3] American Naturalist, Vol. XXIII, pp. 149–151, 1889.

[4] American Naturalist, Vol. XXVII, pp. 659–662, 1893.

[5] Bull. Mus. Comp. Zool., Vol. XX, pp. 99–100, 1890.

labeled with reference to their position in the quarry, in order to trace the different skeletal remains which may continue from one block to another. In working out this material, we find that there are parts of skeletons which are articulated and associated.

As there has been doubt among palaeontologists regarding Professor Marsh's genus Moropus, I decided to present the figures of some casts (Figs. 1–11). These were made, by permission of Professor Schuchert, from the types which were described as bones of edentates by Marsh. By permission of the Authorities of Yale Museum, these types are here illustrated for the first time, and they quite correctly represent the specimens. With the types are associated such specimens of Moropus from the Agate Spring Quarry (Figs. 12–20) as will at once show the characters which are identical.

EXPLANATION OF FIGURES 1–20

All figures $\frac{1}{4}$ *natural size*

Type of *Moropus distans* Marsh. From the John Day Formation, Oregon.

FIG. 1.— Dorsal view of first and portion of second co-ossified phalanges.
FIG. 2.— Proximal articular view of the cuboid.
FIG. 3.— Dorsal view of a second phalanx.
FIG. 4.— Plantar view of the same phalanx.

Type of *Moropus senex* Marsh. From the John Day Formation, Oregon.

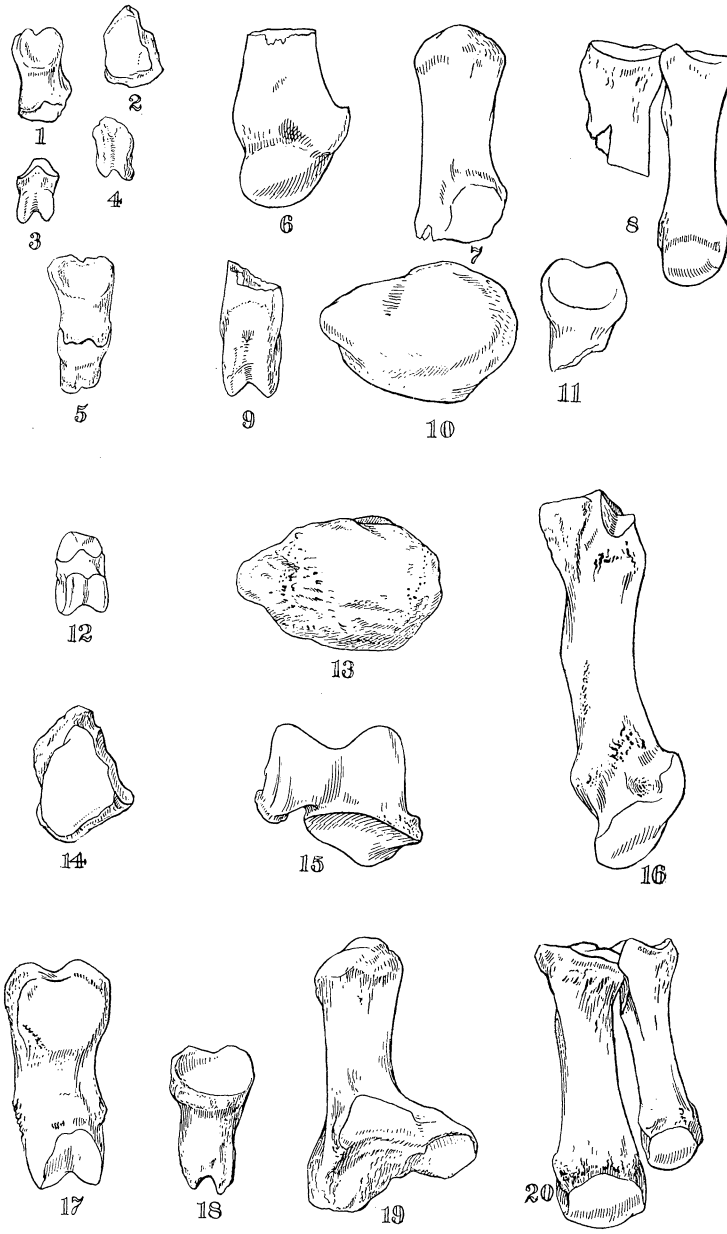
FIG. 5. —Dorsal view of the first and portion of second co-ossified phalanges.

Type of *Moropus elatus* Marsh. From the Miocene of Nebraska.

FIG. 6.— Dorsal view of distal end of second metacarpal.
FIG. 7.— Tuberosity of calcaneum.
FIG. 8.— Dorsal view of metatarsals II and III.
FIG. 9.— Dorsal view of co-ossified first and second phalanges.
FIG. 10.— Dorsal view of patella.
FIG. 11.— Dorsal view showing the proximal end of a first phalanx.

Material of *Moropus elatus* Marsh, from the Agate Spring Fossil Quarry. Miocene of Nebraska.

FIG. 12.— Dorsal view of a second phalanx.
FIG. 13.— Dorsal view of patella.
FIG. 14.— Dorsal view of second metacarpal.
FIG. 15.— Proximal articular view of the cuboid.
FIG. 16.— An oblique view of the astragalus.
FIG. 17.— Dorsal view of co-ossified first and second phalanges.
FIG. 18.— Dorsal view of a first phalanx.
FIG. 19.— Front view of calcaneum.
FIG. 20.— Dorsal view of metatarsals II and III.



FIGURES 1–20.

The skeletal structure of Moropus is a unique combination of characters. The phalanges are highly modified, terminating in cleft ungues which were, no doubt, covered by heavy claws; otherwise the skeleton is distinctively of an ungulate type, most closely resembling the Perissodactyla. The fore limbs are longer than the hind limbs; they, together with the clawed feet, must have given to the animal a very peculiar appearance. Some species are as large as an African rhinoceros, or even larger. In the *American Naturalist*, March 1889, p. 151, Professor Cope established a separate order (Ancylopoda) for these different forms, which in the Miocene time extended over Europe, Asia, and America. After a study of the recently discovered remains, which include nearly all parts of the skeleton, the present writer would place Moropus as a distinct genus, in the Chalicotherioidea which, he is inclined to believe, should be considered as an aberrant superfamily of the Perissodactyla, as it was provisionally regarded by Professor Osborn[1] in a recent publication.

At this point it is thought best to give a short description of a few characteristic features in the osteology of the skeleton of Moropus as we know it from the material in the Carnegie Museum at Pittsburgh.

THE SKULL

No. 1707 Carnegie Museum Catalogue of Vertebrate Fossils.

The skull, on which these brief notes are based, was found in the Agate Spring Fossil Quarry by Mr. W. H. Utterback. It is that of a young individual, which, when found, was disarticulated. We have not, as yet, found a perfect skull of Moropus,[2] but aside from this our material is quite complete. The parts, associated in this skull, but which may not belong to the same individual, are the occipital condyle, the basioccipital (No. 1707 A), and the lower

[1] The Extinct Rhinoceroses. Memoirs of the American Museum of Natural History, Vol. I, Part III, p. 79, 1898.

[2] Professor Barbour of the Nebraska State University, Lincoln, Neb., was fortunate in securing a fairly good skull of Moropus from the same stratum on an adjoining hill.

jaws (No. 1711). The latter parts are here inserted (Fig. 21) in order to give a better idea of the cranium. Since no foot bones were found in connection with these skulls, a positive identification of the species as *elatus* Marsh can not be made.

The skull of Moropus, as a whole, is of the long and narrow type (Figs. 22 and 23) and is in a general way similar to that of Macrotherium of Europe.[1] In this young specimen from Nebraska there is no sagittal crest. The braincase is sub-ovate in form and of fairly large size. The parietal is present on one side and is of

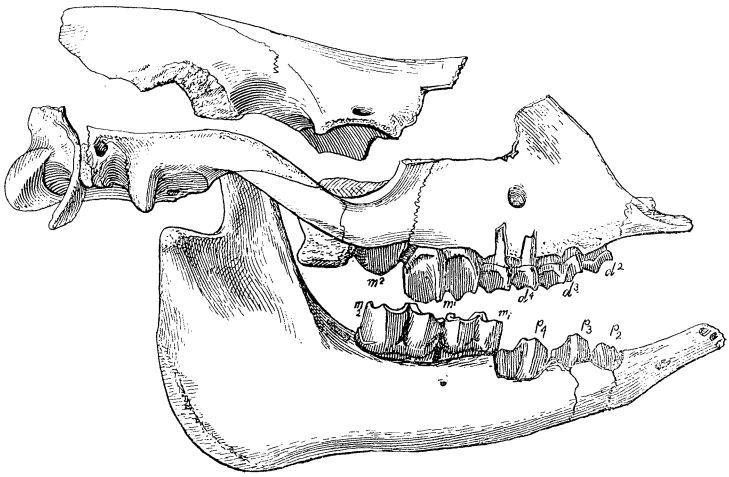


FIG. 21. — *Moropus elatus?* Marsh. ¼ natural size. Side view of the skull of a young individual, No. 1707; side view of the lower jaw of a young individual, No. 1711.

considerable antero-posterior diameter. Superiorly the bone is very gently convex from before backward, and the two parietals together meet the frontals in a broadly open U-shaped outline. The frontal is quite broad over the orbit as in Meniscotherium from the lower Wasatch, and the orbital border is heavy and somewhat overhanging with a large foramen near the margin. This is well shown in the illustrations (Figs. 21 and 22). The supra-temporal ridge is very faint; this may be due to the immaturity of

[1] See Professor Depèret's Memoir "Faune de Mammifères Miocenes de la Greve-St. Alban"; Arch. Muse. d'Hist. Nat. d'Lyon V, Pl. II., 1892.

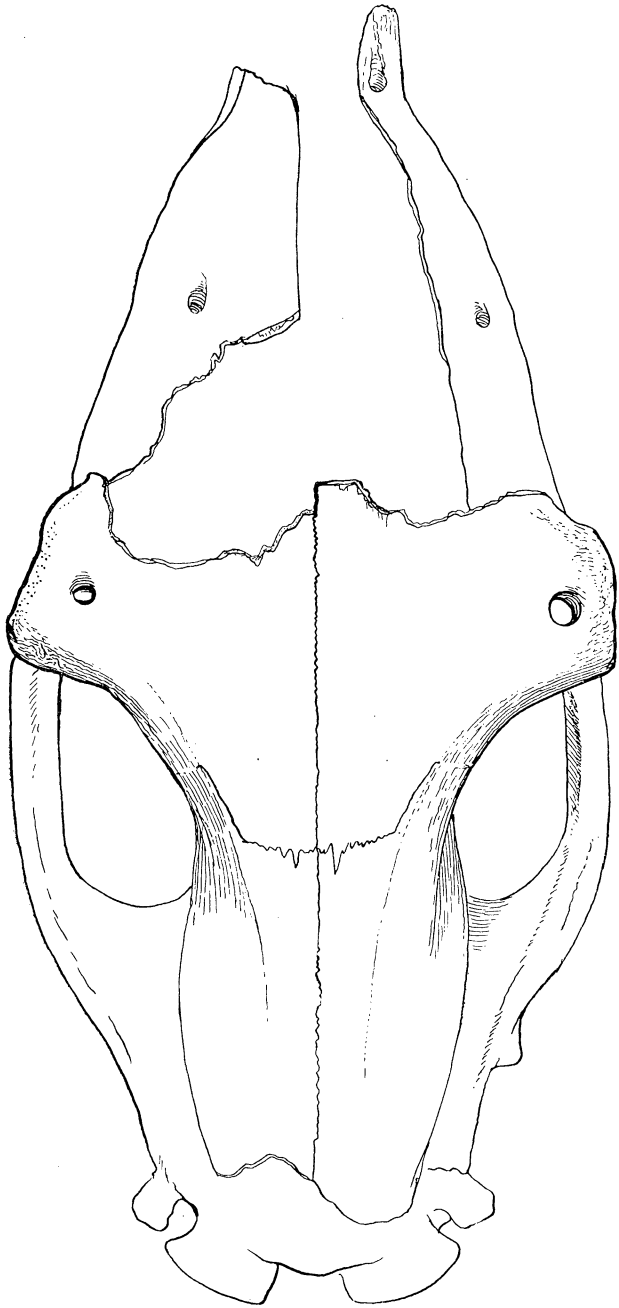


FIG. 22. — *Moropus elatus?* Marsh. ½ natural size. Top view of the skull of a young individual, No. 1707.

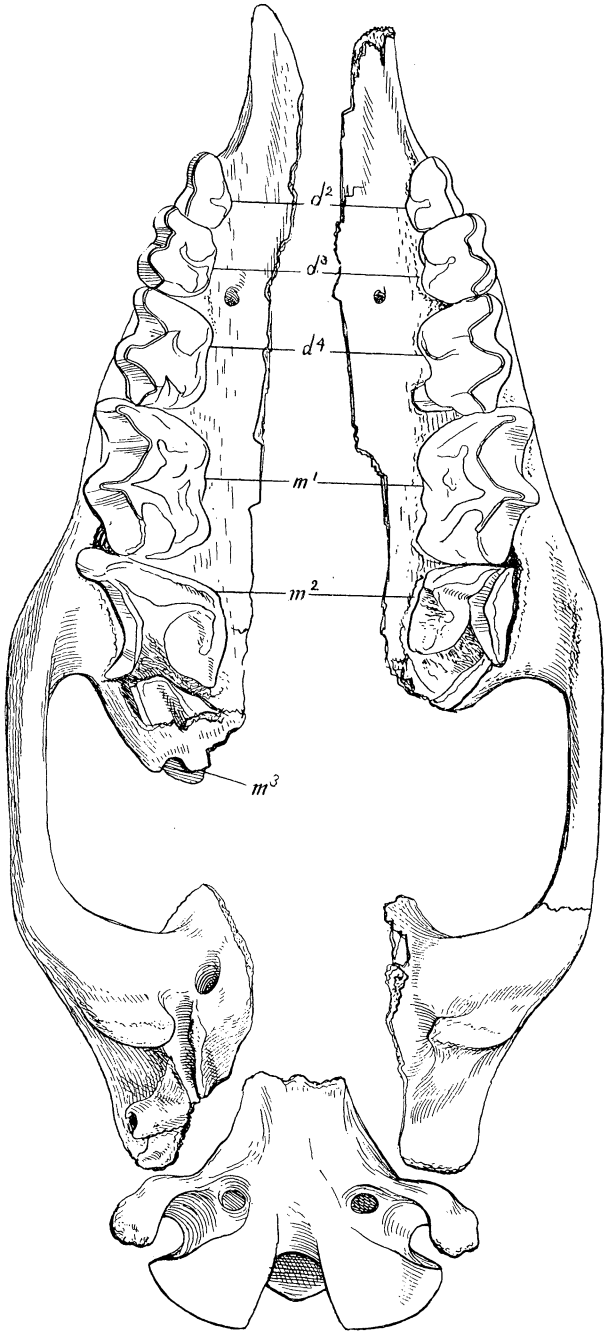


FIG. 23. — *Moropus elatus ?* Marsh. ½ natural size. Palate view of the skull of a young individual, No. 1707.

the specimen, but it continues from the inion to the orbital border. The orbit is located well forward on the skull and is open posteriorly in a similar manner to that of the known European forms. The maxillary bone is high and the maxillo-premaxillary suture ascends rapidly. The premaxillary bone of Moropus is not known, but I judge that it attained a considerable length and was perhaps edentulous or retained small incisors.[1] The infra-orbital foramen is large and is placed above D^4. The jugal is small with a delicate zygomatic process. The zygomatic process of the squamosal is equally small so that the arch is rather more delicate than that represented in the European genus. The glenoid process is of fairly large size and the space between the latter process and

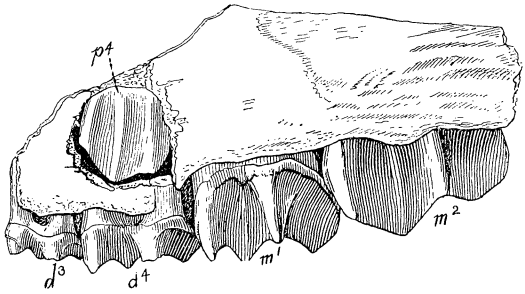


FIG. 24. — *Moropus clatus?* Marsh. ½ natural size. Side view of maxilla of a young individual, No. 1709, showing p^4 in an unerupted stage.

the paroccipital is occupied by the external ear and the mastoid in much the same way as in the recent horse. The external auditory meatus is of fairly large size and is directed outward and very slightly upward, not unlike that in Equus. Whether or not there was a tympanic bulla cannot be determined from the material at hand. The occipital condyle is large and there is a slight accessory facet on the basioccipital. The condylar foramen is of large size and is situated immediately back of the paroccipital process at its internal angle. The latter process is much elongated and suggests that of the recent horse. In fact a number of osteological features of Moropus suggest characters in the equine family of the Perissodactyla.

[1] Lower jaws of adults with incisors in place always show wear on the median pair, while the lateral teeth are almost entirely unworn.

The molar-premolar series of Moropus has a general similarity to that of the Titanotheres, but a brief comparison of the more important differences is thought to be of interest in this connection. The external walls of the upper premolars of Titanotherium are excavated, forming a transverse median valley on the grinding face of the teeth, while in Moropus the walls are highest in the middle, and this portion of the tooth is not divided by a transverse valley. The internal cusps of all the upper premolars in Titanotherium have a tendency to become divided so as to form a larger anterior and a smaller posterior tubercle. In Moropus the single tubercle is crescentic, especially on P^4. On the molars of Titanotherium there are two distinct internal tubercles, while in

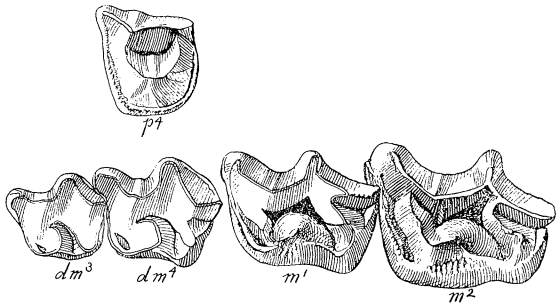


FIG. 25. — *Moropus clatus?* Marsh. ½ natural size. Crown view of the same specimen as Fig. 24.

Moropus there is only one tubercle and a transverse cutting lobe on the posterior internal angle of the tooth. This transverse lobe which unites with the external part of the tooth has apparently taken the place of the posterior internal tubercle (hypocone) of Titanotherium and is similar to that of Meniscotherium as was pointed out by Professor Osborn in comparing the latter with the known genera of the Chalicotherioidea.[1] The upper molars in Moropus are relatively longer and narrower than in the Titanotheridae; they are also longer and narrower than the upper molars of the best known forms of Chalicotherioidea in Europe and Asia.[2]

[1] American Naturalist, Vol. XXVII., p. 127, February, 1893.

[2] On Plate III., figs. 3, 4, and 5 in Depèret's Memoir, l. c., are figures of upper molars which more nearly agree in diameter with those of Moropus.

The close similarity of the lower molar-premolar series of Chalicotherioidea to that of Titanotherium and Palaeosyops is well known. As in the European forms, the present genus has also the premolars reduced to three teeth in both upper and lower jaws, while in the Titanotheridae there are four. P_2 in Moropus is quite simple in structure, while P_3 is more nearly like P_2 in Titanotherium. The internal tubercle of P_4 in Moropus is somewhat heavier than that in Titanotherium, otherwise the tooth suggests that of the latter genus. M_1 and M_2 in Moropus are similar to those in Titanotherium. M_3 in the latter genus has a prominent posterior heel which is lacking in Moropus. This third lobe of M_3 is also lacking in the Wasatch genus Meniscotherium.

The deciduous upper molars (No. 1709) in Moropus are more nearly molariform than are the permanent premolar series.[1] Deciduous M^4 (d^4 and dm^4 in Figs. 24 and 25 respectively) may very easily be taken for the permanent M^1, if extreme care is not exercised in the study of the dentition. The permanent P^4 cuts the alveolar border shortly after permanent M^2 is entirely erupted.

MEASUREMENTS OF THE SKULL

	mm.
Diameter of skull, from external auditory meatus to extreme anterior point of maxillary,	305
Diameter of skull, from external auditory meatus to anterior border of the orbit,	160
Diameter of skull, from anterior border of the orbit to extreme anterior point of the maxillary,	150
Transverse diameter of the frontals over the orbits,	160

VERTEBRAL COLUMN

No. 1604, Carnegie Mus. Cat. Vert. Foss.

The vertebral formula of Moropus is for the most part based on a skeleton, the bones of which were found disarticulated, but

[1] Hatcher has pointed out this same characteristic feature in Titanotherium, Annals Carnegie Museum, Vol. I, pp. 259–260, 1901.

quite close together, in the Agate Spring Fossil Quarry. As the vertebrae are found to fit one another in a quite perfect manner, there is very little doubt that the cervicals and the dorsals are, excepting the eighth and eleventh dorsals which are evidently lost, correctly represented by this specimen. We found seven cervicals, thirteen dorsals, and three anterior lumbars belonging to the same individual. The cervical and dorsal regions are apparently quite complete, while three lumbars are lacking, but judging from other individuals found in the quarry the complete number in the lumbar series was six. There was no sacrum with this individual, but we know that there are four sacral vertebrae. The caudal region is not fully known, but I judge that it attained a length about equal to that in the rhinoceroses generally.

The Cervical Vertebrae.— For an animal with a comparatively small head, the cervical vertebrae of Moropus are quite robust. The general structure of the cervical region suggests that of the recent horse. With the exception of the greater angularity of the transverse process, the different position of the arterial canal and the open atlanteal notch, the atlas might be taken for that of a large specimen of *Equus caballus*. The axis is still more suggestive of the horse, but the inferior keel is larger and the neural spine higher,[1] more overhanging in front, and somewhat more robust. The articulation for the atlas has the same spout-shaped extension anteriorly, but with the median protuberance relatively much enlarged, forming a curious knob which doubtless represents the primitive odontoid process. With the exception of the more produced condition of the centra posteriorly, the more broadly developed hypapophysial keels inferiorly, the higher neural spines, the relatively heavier neural arches, and the larger zygapophysial faces, the general make-up of the cervicals back of the axis in Moropus is similar to that in Equus. There is no vertebrarterial canal in the seventh cervical. That the animal could easily reach the ground with his head is very evident from similarities of the cervical articulations to those of *Equus caballus*.

[1] The axis of Macrotherium of Europe is described and figured by Professor Depèret and presents the same general characters as that in the American species. The neural spine of the former is relatively higher than that in the latter species.

The Dorsal Vertebrae. — Although the number of the dorsal vertebrae in Moropus is less (there are thirteen present and two — the eighth and eleventh dorsals — lost in the specimen under consideration) they are perhaps more suggestive of those of Aceratheria or Metamynodon from the Oligocene than those of the horse. The first dorsal in Moropus has a relatively longer neural spine than that in the horse, and in this respect it resembles more nearly some of the more primitive perissodactyls. The seventh, ninth, and tenth dorsal vertebrae in No. 1604 have complete neural spines. It is seen that the neural spines of the latter vertebrae are relatively shorter and have a more backward slope than in the horse. The thirteenth and fourteenth dorsals have wide neural spines, which are constricted antero-posteriorly at their bases. In these vertebrae there are strong metapophyses. The fifteenth dorsal vertebra in Moropus is quite characteristic and is different from all preceding vertebrae. The posterior zygapophyses have already become convex in the same manner as in the lumbar region.

The transverse process is pierced at the base by a large foramen and is further characterized by having a superior and an inferior division. The superior division of the transverse process is the larger of the two and is directed outward, while the smaller inferior division has a downward and backward direction. Between the two divisions there is a deeply emarginated area, which is converted into a thin bony bridge bounding the foramen referred to above. On this and the succeeding vertebra (the first lumbar) the metapophyses are the heaviest and they rapidly decrease in size on the succeeding lumbars, while on the dorsals there is still a very small metapophysial protuberance left on the seventh vertebra.

Only the first three lumbar vertebrae are present in No. 1604, the specimen under consideration, but from other material found in the quarry it is quite certain that the complete series is six. The three lumbars present are very robust, and possess broad neural spines which are enlarged and rugose at the superior end. The zygapophyses are simply convex and concave with no additional superior articular faces. The transverse processes are only moderately developed.

The Sacrum. — The sacrum (No. 1706) is composed of four

vertebrae well co-ossified, with high and backwardly sloping neural spines which are all co-ossified and increase in robustness from before backward. The neurapophysis of the first sacral is very heavy and supports the greatest weight of the ilium, though the succeeding three sacrals share in the support as there is a rugose attachment for the ilium throughout the entire length of the sides of the sacrum.

A number of caudals of considerable length, found in the quarry, may belong to Moropus but this is not fully determined at present.

In No. 1604, Car. Mus. Cat. Vert. Foss., the best preserved skeleton of Moropus, there are present fifteen ribs of the right and fourteen of the left side; the first rib of the left side is lost. The ribs are of moderate length, but robust, and the anterior ones are expanded at the lower ends, indicating a heavy sternal attachment.

Limbs

Nos. 1604; 1706; 1710; Carnegie Mus. Cat. Vert. Foss.

The structure of the fore and hind limbs of Moropus was briefly described in a former paper,[1] and I wish here only to call attention to a few of the more important features which are shown in the splendidly preserved material in the Carnegie Museum.

The Fore Limb.— The scapula of Moropus is quite large. It is plainly of a perissodactyl type, and resembles most closely that of *Aceratherium tridactylum* Osborn. As in the latter genus the spine is prominent and overhangs the post-scapular fossa in a similar manner. The humerus, radius, and ulna of Moropus, as a whole, are quite like these parts in the European genera.[2] The humerus of Moropus has a heavy deltoid ridge, which extends well down on the shaft. The greater tuberosity is also quite robust and the bicipital groove is single and moderately deep, but quite broad. The distal end is much expanded transversely and suggests that of

[1] Annals Carnegie Museum, Vol. IV, No. I, pp. 60–61, 1906.

[2] In *Macrotherium grande* the fore limb is relatively longer than in Moropus according to the figures and description of Professor Depèret, "La Faune de Mammifères de la Greve-St. Alban" Pl. IV, Figs. 2 and 9.

Phenacodus from the Wasatch. The trochlea is broad with well rounded articular surfaces for the radius and ulna. The anconeal fossa is quite deep and broad, but low. In this specimen (No. 1604) the radius and ulna are entirely co-ossified. On the radius the external articular facet for the humerus is considerably larger than the internal, while on the ulna the internal articulation is very extensive. On a direct front view the head of the radius lies in front of the ulna, but immediately below the head on the external side, the shaft of the ulna again appears. The olecranon of the

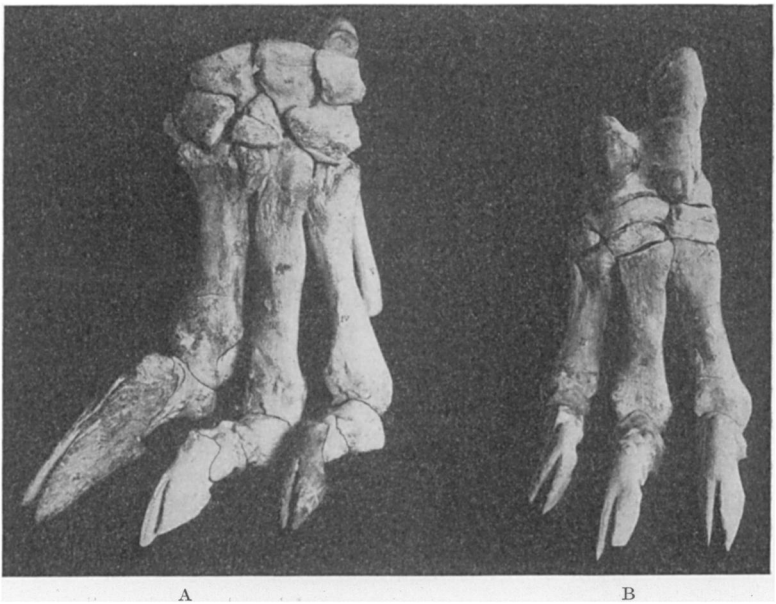


FIG. 26. — *Moropus elatus* Marsh. About $\frac{1}{8}$ natural size. A, the left fore foot of skeleton No. 1604. B, the left hind foot, No. 1710, which belongs with another skeleton.

ulna is rather truncated. The distal end of the radius and ulna together have a transversely broad aspect; the carpal articulation is characteristically plain without the prominent border which separates the scaphoid and lunar facets in other Perissodactyla. The articular surface for the cuneiform on the ulna project only very slightly below the radius and form, with the lunar articulation on the radius, a continuous and gently curved surface. The suture

between the radius and ulna is, however, well indicated on the distal articulation of the bone.

The Manus.— The manus of Moropus has four digits, three of which are functional and one (the fifth) rudimentary. This rudimentary fifth metacarpal is not supported by the unciform, but articulates with the fourth metacarpal by fairly well formed facets. Mc.V [1] in No. 1700, Car. Mus. Cat. Vert. Foss., is much slenderer and attains only three-fourths the length of mc. IV. The distal trochlea of mc. V., in No. 1700 is quite imperfect and the digit had perhaps only one phalanx. The trapezium is present and articulates with mc. II, the trapezoid, and the scaphoid, but there is no indication of a first digit. The heavy protuberance on the scaphoid of Moropus which reaches over the trapezoid and articulates with the magnum may be represented by the centrale in Meniscotherium.[2] The magnum has a heavy protuberance on the anterior face which extends dorsally and forms, on the distal face, a rough articular surface for the proximal end of mc. II; on the palmar face is a short but heavy hook, and the total vertical diameter of the bone is much greater than is apparent on a direct front view of the manus. The second metacarpal, though shorter than the third and fourth, is the heaviest in the series. The third metacarpal is the longest, consequently the second and third digits in the manus of Moropus supported the greatest weight; therefore the manus is more nearly mesaxonic than was anticipated. It is different from the European genus from Sansan in which mc. IV is the longest.

In the manus of Moropus, the first and second phalanges of the second digit are co-ossified, an important character which Professor Marsh luckily discovered in three different individuals. This now proves to be of perhaps a family importance.[3] The ungual phalanx of the second digit is much larger than those on the third

[1] In No. 1604 the fifth metacarpal is wanting, but the articular facets of mc. IV plainly indicate its presence.

[2] Amer. Jour. Science, Vol. XLIII, p. 447, 1892. (*Hyracops socialis* Marsh.)

[3] From Cope's statement in the American Naturalist, March, 1889, Vol. XXIII, p. 153, I infer that Lydekker has said that "Ancylotherium" Gaudry has the first and second phalanx co-ossified. Good casts of the latter genus are exhibited in the American Museum of Natural History which confirm this statement.

and fourth, and is more conspicuous than that of the European form from Sansan. In Moropus as in "Ancylotherium" this large ungual has a comparatively limited dorsal flexure, as there is a shoulder near the dorsal border of the distal trochlea of this duplex bone and a corresponding buttress on the articulation of the terminal phalanx; thus furnishing additional strength in the use of this digit.

Hind Limb.—The pelvis (No. 1706) of Moropus may be regarded as long and narrow. In comparing it with that of Perissodactyla generally it is relatively longer in the region back of the acetabulum, which feature is artiodactyl rather than perissodactyl. Altogether, the pelvis of Moropus most nearly agrees with that of *Aceratherium tridactylum*. As in the latter genus, the neck of the ilium is long with a rapid expansion near the supra-iliac border, but this border is less emarginated than in Aceratherium. In Moropus the acetabulum is deep, and the pit for the round ligament is of large size and is confined to the region back of the median line. The obturator foramen is ovate in outline and of medium large size. The pubic symphysis is quite strong anteriorly, but in No. 1706, Carnegie Museum Cat. Vert., Foss., the ischium diverges outwardly more than is usual in other specimens.[1] As stated elsewhere, the femur has a strong third trochanter, which is located above the middle of the shaft. The bone as a whole resembles that of Titanotherium, but is relatively heavier and shorter. The tibia is short and heavy; it is about four-fifths the length of the femur. The articular facets for the femur are divided by a prominent spine, the cnemial keel is heavy and extends well down on the shaft, and the distal trochlea is characteristically rhinocerotic. The fibula is complete, but its shaft is comparatively delicate and has an even curvature from above downward so that it lies close to the shaft of the tibia throughout; the distal end extends below the external articular facet of the tibia and articulates with the astragalus, but does not always touch the calcaneum.[2]

[1] The peduncle of the pubis in this specimen was badly crushed on one side and partly lost on the opposite side which may, in part at least, account for this difference.

[2] Some specimens have a minute articular facet for the fibula on the calcaneum.

The Pes. — In a general way the tarsus (No. 1710) in Moropus is much like that of the Rhinocerotidae. There are, however, many differences viz: the navicular is supported entirely by the astragalus and the cuboid by the calcaneum as in Meniscotherium. The trochlea of the astragalus is somewhat more deeply grooved, the internal and external condyles are more even in size and the external condyle is not interrupted as in Titanotherium, but continues below the articular facet for the navicular. The pes is tridactyl; there is no indication of lateral digits. The second metatarsal is shorter and also somewhat lighter than the third and fourth which are of equal size. The articulation for the proximal phalanx is confined almost entirely to the dorsal face of the bone, while on the plantar face are deep, broad grooves, which are divided by heavy keels. The sesamoids are very heavy and in some cases they are co-ossified, forming a broad open groove for the tendons. As in the fore foot the claw-bearing ungulae are deeply cleft, but of more nearly equal size.

From the study of the foot and limb structure of Moropus it is very evident that the animal was digitigrade. Professor Osborn has called attention to the fact that the European forms were "almost certainly sub-digitigrade."[1]

The remains above described (No. 1604) belong to an individual very nearly the size of *Chalicotherium goldfussi* of Europe, or the size of a small specimen of Titanotherium from the American Oligocene. Smaller remains are more common in the quarry, indicating two or more species, or a great range of individual variation. This question will be taken up in a later publication. There are perhaps twenty individuals of Moropus represented in the collection of the Carnegie Museum, which were secured in the Agate Spring Fossil Quarry.

Discussion of Affinity and Phylogeny

In *Chalicotherium goldfussi* Kaup, P^4 has the internal face of the ectoloph W-shaped and the internal tubercle of a different form and more distinctly separated than in the American genus. In the

[1] American Naturalist, Vol. XXVII, pp. 118–119, 1893.

latter, the ectoloph is simpler, and the internal tubercle is crescentic, as in the Artiodactyla, the posterior and anterior horns being firmly united with the ectoloph so as to form, of the median valley, a deep, but rapidly sloping pit. This is best seen in an unworn tooth. The upper molars, especially M^2 and M^3, in Moropus are relatively longer and narrower than in *Chalicotherium goldfussi*. The teeth in the latter species appear to have more nearly the same proportionate diameter as in the Asiatic forms *C. siense* and *C. sivalense*.[1] The more important differences between *C. sivalense* and *C. siense* as pointed out in Professor Owen's paper (l. c. pp. 431–432) are as follows: "the anterior part of the interval between the post-external (b) [b = reference to the illustrations in Owen's paper] and the postinternal (d) lobes is not closed by a ridge descending from the summit of the postexternal lobe as in *Chalicotherium sivalense*: nor does the inner side of the antexternal lobe terminate in so ridge-like a way as in *Chalicotherium sivalense*." The condition of the post-external and post-internal lobes, as well as the "ridge-like" ant-external lobe of M^3 in Moropus agree more closely with Owen's statement of *C. sivalense*; and M_3 in Moropus is very nearly of the same size and of the same general character as that in *C. goldfussi*, but the relative diameter,[2] together with other less important differences of M^3 in the European and Asiatic forms, is entirely unlike those in Moropus.[3]

Phylogeny.—The best evidence at the present time points rather towards a European[4] than an American ancestry of Moropus.

[1] Quart. Jour. Geol. Society, London, Vol. XXVI, p. 431, 1870.

[2] For measurements of upper teeth of Moropus see Annals Carnegie Museum, Vol. IV, No. I, p. 63, 1906.

[3] *Chalicotherium* (*Ancylotherium*) *pentelici*, from Pikermi, Greece, has the upper molars longer than broad, and in some other respects most nearly agree with the American form.

[4] Schizotherium Gaudry of the European Oligocene is undoubtedly an ancestor of the family. And it is likely that some European Eocene form allied to the early perissodactyls will be found to be the true ancestor. Some characters of Palaeotherium are suggestive of the Chalicotherioidea.

NOTE: While at the International Zoological Congress in Boston, I discussed the phylogeny of Chalicotherioidea with Professor Depèret who kindly added the following note: "Le plus ancien type européen des Chalicotherioidea est le Pernatherium Gervais, du calcaire de St. Ouen près Paris: il est de l'étage Bartonien, c'est à dire, à peu près du Bridger supérieur (voir Journal de Zoologie.)"

Professor Osborn has pointed out Meniscotherium from the American Eocene (Wasatch) as a possible ancestor of the Chalicotherioidea.[1] It would seem that when better specimens of *Moropus distans* are found in the John Day formation, it will become necessary to separate, generically, *Moropus elatus* from *Moropus distans*. "*Chalicotherium bilobatum*" Cope from the Oligocene of the Swift Current Creek in Canada, if correctly identified, is of course a much earlier form than *Moropus elatus* from the Miocene of Nebraska. The remains which Professor Scott reports from Montana (Deep River) may perhaps represent a transitional form between *Chalicotherium bilobatum* and *Moropus elatus*. These appear to be the evidence which we have of the presence of the chalicotheres in the American Tertiary. The little known *Spenocoelus wintensis* Osborn from the Uinta beds[2] bears some resemblance to the Chalicotherioidea as was pointed out by Osborn (l. c. p. 102), but the specimen (the posterior portion of the skull) is too imperfect for accurate comparison. While Meniscotherium may not be a true ancestor of Moropus there are in the latter certain affinities[3] to the former which are of much importance and which point to the ancestral types of the stem of the Perissodactyla.

Conclusion

The conclusions drawn from the material studied may be summed up as follows: (1) That Moropus is, excepting its unguiculate feet, essentially a perissodactyl in structure. (2) That the laterally compressed and cleft condition of the terminal phalanges is quite distinct in some of the early Perissodactyla,[4] and that by adaptation through geological ages the unguals as well as other parts of Moropus were specially modified, and should not, in the mind of

[1] American Naturalist, February, 1893, pp. 118–133.

[2] Bull. American Museum of Natural History, Vol. VII, pp. 98–102, 1895.

[3] The absence of the 3rd lobe of M_3; the 3rd trochanter of the femur, and the navicular articulating, proximally, only by the astragalus and the cuboid by the calcaneum.

[4] It is well known that Euprotogonia and some species of Phenacodus have the terminal phalanges laterally compressed, intermediate between hoofs and claws. The early horses have cleft ungues.

the writer, be regarded as of ordinal importance. (3) That Moropus is generically separable from other known forms of the Chalicotherioidea.

The illustrations are from drawings made by Sidney Prentice and photographs made by A. S. Coggeshall.

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